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FISHES OF THE DARKNESS

Water colour-regulated competitive interactions in humic lakes

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ACADEMIC DISSERTATION

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ABSTRACT

Humic lakes are abundant in the temperate and cold regions of the Boreal Zone. High levels of water colour and strong thermal stratification of humic lakes limit the potential fish habitats and give a special role to the intraspecific and interspecific interactions. Water colour has different effects on species depending on species-specific life-history traits and trophic interactions. Fish species whose success in predation is based on visual cues are more susceptible to suffer in competition.

The main aim of the thesis was to demonstrate the effects of water colour on European perch (*Perca fluviatilis*) in humic lakes. The contribution of water colour to diet, feeding, growth and competitive interactions of fish was studied both in laboratory and in small humic lakes with varying levels of water colour.

The main findings of the thesis were that water colour has different effects on species, depending on species-specific life-history traits and trophic interactions. Water colour affected visually-oriented perch feeding and growth negatively, and the prolonged benthic feeding phase of perch resulting from the increased water colour could increase intraspecific competition in perch populations and may result in a partial bottleneck in growth for perch. Moreover, water colour may act as a proximate factor behind the population dependency of sexual growth dimorphism in perch

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List of Original publications

This thesis is based on the following articles referred to in the text by Roman numbers (I–V)

- I** Estlander S, Nurminen L, Olin M, Vinni M & Horppila J 2009. Seasonal fluctuations in macrophyte cover and water transparency of four brown-water lakes – implications for crustacean zooplankton in littoral and pelagic habitats. *Hydrobiologia* 620: 109–120.

- II** Horppila J, Olin M, Vinni M, Estlander S, Nurminen L, Rask M, Ruuhijärvi J, Lehtonen H 2010. Perch production in forest lakes: the contribution of abiotic and biotic factors. *Ecology of Freshwater Fish* 19: 257–266.

- III** Estlander S, Nurminen L, Olin M, Vinni M, Immonen S, Rask M, Ruuhijärvi J, Horppila J & Lehtonen H 2010. Diet shifts and food selection of perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*) in humic lakes of varying water colour. *Journal of Fish Biology* 77: 241–256.

- IV** Estlander S, Horppila J, Olin M, Vinni M, Lehtonen H, Rask M & Nurminen L 2011. Troubled by the Humics – Effects of water colour and interspecific competition on the feeding efficiency of planktivorous perch. *Boreal Environment Research* (accepted after revision)

- V** Horppila J, Estlander S, Olin M, Pihlajamäki J, Vinni M & Nurminen L 2011. Gender-dependent effects of water quality and conspecific density on the feeding rate of fish – factors behind sexual growth dimorphism. *Oikos* 120: 855–861.

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Contribution of authors

	I	II	III	IV	V
Original idea	SE, LN	JH, MO, HL	SE	SE, LN	SE
Study design	SE, LN	JH, MO	SE, LN	SE, LN, JH	SE, LN, JH
Data collection	SE, MV, MO	SE, MO, MV, HL, MR, JR	SE, MV, MO, HL, SI, MR, JR	SE, LN, MV, JP, MO, MR	SE, LN, MO, JP, MV,
Data analysis	SE, JH	MO, JH	SE, MV, JH	SE, LN	JH, SE
Manuscript preparation	SE, JH, LN, MO	JH, MO, SE, LN	SE, LN, JH, MO, MV	SE, LN, JH	JH, SE, LN

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1. Introduction

1.1 Characteristics of humic lakes

Humic lakes are abundant (Kortelainen 1999) in the temperate and cold regions of the Boreal Zone. For example, in Finland the average water colour of lakes is ~ 100 mg Pt l⁻¹ and > 60% of lakes have relatively high humus content, enough to stain the water colour to that of dark beer (Kortelainen et al. 2004). These lakes have high surface water temperatures (up to 28 °C) during summer, but are covered with ice from November until April (Rask et al. 1992; Keskitalo & Eloranta 1999; Järvinen et al. 2002). The humic substances of dissolved organic compounds are the major factor controlling water colour in lakes (Thurman 1985; Pace & Cole 2002). Since humic substances absorb light very effectively, they strongly affect light attenuation but have little effect on light scattering, in contrary to suspended particles in turbid waters (Kirk 1994). In highly humic lakes, ecosystem productivity is strongly restricted, due to strong light extinction in the water column. Small humic lakes in Finland are usually polyhumic and have relatively low pH and naturally low oxygen in the hypolimnion during summer and winter stagnation (Kortelainen et al. 2004).

Since water colour not only influences light penetration, but also the vertical profiles of temperature and oxygen, strong thermal stratification is typical in humic lakes during the growing season. Strong thermal stratification produces a barrier for oxygen transport from the epilimnion to the deeper water layers, and increased oxygen consumption, due to high concentration of organic matter, very often causes oxygen depletion in the hypolimnion. These physical attributes have a remarkable influence on the food webs of humic lakes. Such characteristics limit potential fish habitats and give a special role to intraspecific and interspecific interactions (Crowder & Cooper 1982; Chick & McIvor 1994; Holmgren & Appelberg 2000; Lewin et al. 2004).

European perch (*Perca fluviatilis* L.) is often the dominant fish species in small Nordic forest lakes (Rask et al. 2000). In many lakes, it is the only fish species present or co-occurs with few other fish species, most often with roach (*Rutilus rutilus* (L.)) and northern pike (*Esox lucius* L.). The growth rate of fish in humic lakes is usually slower than in clear lakes, which is attributed to poor light conditions that result in low predation efficiency and low hypolimnetic oxygen concentration that reduces the number of potential habitats and increases competition for available resources (Rask et al. 1999). On the other hand, some studies have suggested that the biomass of fish in humic lakes may not be dependent on water colour but rather on population density and food availability (Rask et al. 1999).

The issue is complex, because water colour in turn affects food availability through its effects on light extinction and thus on the overall ecosystem productivity, while allochthonous humic substances are an important source of carbon and energy (Salonen et al. 1983).

1.2 Fish predation – special features of humic lakes

Fish predation has been cited as one of the most important factors influencing zooplankton community structure (Brooks & Dodson 1965) and distribution (Urabe 1990). In addition to fish, many invertebrates are also predators that prey on zooplankton. For example, chaoborids can modify the effects of fish predation on zooplankton by competing with fish for zooplankton and by acting as prey for planktivorous fish (Persson et al. 1992; Pekcan-Hekim et al. 2006). According to the balanced predation hypothesis (Dodson 1974), the size structure of the zooplankton community is the result of a balance between fish and invertebrate predation.

High water colour can enhance a refuge in which prey can avoid fish, since fish are mostly visual predators whose feeding rate is strongly dependent on the water clarity (Vinyard & O'Brien 1976; Confer et al. 1978). High water colour may also reduce prey selectivity in fish. Vinyard & O'Brien (1976) showed that planktivorous fish generally select positively for larger zooplankton individuals under favourable light conditions, but at low light the size selectivity is weaker. Due to the effects of water colour on fish feeding efficiency and selectivity, zooplankton individuals should on average be larger in high-colour lakes than in lakes with low water colour (Wissel et al. 2003).

To counteract predation, zooplankton can decrease the predation threat by performing vertical migrations between feeding layers near the surface and refuges in deep, dark waters (Lampert 1993). Large-sized prey items can also escape fish predation by inhabiting low-oxygen areas (Sih 1987; Hanazato et al. 1989; Wright & Shapiro 1990). The experimental study of Liljendahl-Nurminen et al. (2008) showed that a combination of two different types of refuges – physiological (low oxygen) and visual (turbidity) – can create effective shelter against fish predation. In humic lakes, both refuges are commonly available: low oxygen concentration and low light intensity.

Zooplankton can also avoid fish predation by performing horizontal migrations in weedy littoral zones (Davies 1985). The feeding efficiency of planktivorous fish is usually lower among vegetation than in the open water, due to the structural complexity of macrophyte areas (e.g. Winfield 1986; Jeppesen et al. 1997). Due to strong light attenuation, the littoral vegetation zone in highly humic waters is usually narrow and submerged vegetation is sparse (Middelboe & Markager 1997). However, humic lakes often show dense beds of floating-leaved and emergent macrophyte species that may be important refuges for zooplankton against fish predation (Timms & Moss 1984; Nurminen et al. 2001, 2007). Some studies have indicated that the importance of structural complexity as a refuge is dependent on water quality. It has been shown, for instance, that the refuge effect of macrophytes decreases when clay turbidity increases (Snickars et al. 2004; Pekcan-Hekim 2007).

1.3 Fishes of darkness – competitive interactions between perch and roach

Fish inhabit a whole scale of light environments in natural waters and their visual adaptation varies considerably from species to species (Wootton 1990). Some species, such as roach are known to be active in foraging at low light intensities (Zadorozhnaya 1978; Lammens et al. 1987; Diehl 1988; Van Den Berg et al. 1994), while some species prefer well-lighted conditions and feed actively during the day (e.g. perch) (Vinyard & O'Brien 1976; Ali et al. 1977). Previous studies have shown that decreased visibility severely disturbs prey detection by visually oriented fish (Vinyard & O'Brien 1976; Nurminen & Horppila 2006). Water colour may thus reduce fish feeding efficiency and prey selectivity. Several studies (Gregory 1993; Abrahams & Kattenfeld 1997; Horppila et al. 2004) have also shown that decreased light can lead to enhanced feeding activity caused by a reduced risk of predation.

Perch and roach are widely distributed throughout Europe and are the two most abundant fish species in most lakes in Finland. Living together, perch and roach compete for food, especially at the small planktivorous stage (Persson 1990; Persson & Greenberg 1990; Persson et al. 1999). Field studies of size-structured fish populations suggest that competitive bottlenecks are common (Keast 1977; Persson 1983; 1987; Werner 1986; Persson & Greenberg 1990). For instance, species A must pass through a zooplankton feeding stage before they become piscivorous as adults. Young individuals of species A utilize resources similar to those used by species B which are specialized planktivores (i.e. highly efficient planktivores as adults). Therefore, interspecific competition during the juvenile stage of species A may reduce recruitment to larger size classes, resulting in a juvenile competitive bottleneck (Persson 1986; Werner 1986). The perch population growth bottleneck is generally explained by this theory.

Persson and Greenberg (1990) showed that perch are inferior foragers on zooplankton compared with roach. As perch grow, they switch to larger food items, such as benthic macroinvertebrates, and finally turn to piscivory (Allen 1935). Therefore, interspecific competition for zooplankton with roach forces young perch to switch to benthic food at a relatively early age, which increases intraspecific competition in perch populations (Persson 1986). Furthermore, competition reduces the growth rate of perch individuals and delays or prohibits their shift to the piscivorous stage (Persson & Greenberg 1990). Additionally, roach are known for their capability of efficient foraging in simple-structured habitats (Persson 1987), whereas perch prefer structural complexity, e.g. as provided by macrophytes (Diehl 1988). In humic lakes, structured habitats such as those provided by macrophytes are often limited to narrow littoral areas due to the lack of light (Chambers & Kalff 1985).

Decreased light intensity in water may affect the competitive interactions between perch and roach, since these species are adapted to a particular light climate (Henderson & Northcote 1985; O'Brien 1987). In addition, the competition between perch and roach often favours roach over perch (Persson 1987). This is generally explained by the wider food spectrum of roach, i.e. to their ability to use detritus and primary producers as a competitive refuge (Persson 1983). Moreover, recent studies conducted in humic lakes suggest that roach may have a more negative effect on perch growth in lakes with high water colour than in clearer lakes (Olin et al. 2010). These competitive interactions are often complex, since species can be competitors, predators and prey, depending on their sizes (e.g. Werner & Gilliam 1984; Hairston 1986; Holmuzki 1986; Wilbur 1988).

Changes in fish feeding efficiency may also have far-reaching and cascading consequences on population levels. It has been shown that feeding level may affect the growth differences between males and females. Fontaine et al. (1997) suggested that variations in feeding rate may lead to sexual growth dimorphism in perch, the growth rate of females decreasing more steeply than the growth rate of males when the feeding rate decreases. Since perch are visual predators, high water colour may affect sexual growth dimorphism through effects on the feeding rate of perch. Sexual growth dimorphism is usually attributed to taxa, in which the reproductive success of females increases more rapidly with size than that of males (Henderson et al. 2003). This female-biased growth is a crucial factor in formulating the community structure of fish populations, since large females are especially important in regulating the reproductive success of fish populations (Birkeland & Dayton 2005).

2. Objectives and hypotheses of the thesis and original articles

The present study was part of the SUSFISH project (“Principle of Sustainable Fishing in Fish Stock Management”, www.helsinki.fi/keskala), which was designed to clarify the structure and function of humic lake food webs from the perspective of fisheries management. The main aim of the thesis was to demonstrate the effects of water colour on perch in humic lakes. The thesis is composed of five studies, all of which are associated with water colour and perch (Fig. 1). The first two articles (**I** & **II**) describe the biotic and abiotic variables, zooplankton resources and perch production in the study lakes. In the first article (**I**) the aim was to clarify the effects of water colour and littoral macrophytes on seasonal zooplankton distribution. The refuge effect of water colour for zooplankton against predation was also evaluated and discussed. The objectives in **II** were to explore the biomass, growth and production of perch in the study lakes, the contribution of abiotic and biotic factors to the regulation of perch productivity was also explored. In **III**, the coexistence, food selection and diet of perch and roach in lakes with varying levels of water colour were investigated. To verify the results from field studies, experimental laboratory studies were conducted, in which the effects of increasing fish density and the disturbing role of roach on the feeding rate of planktivorous perch were examined (**IV**). Finally, in paper **V** was studied, whether the effects of increasing water colour and increasing population density on the feeding rate of individual perch are gender-dependent.

This thesis focuses on the following questions:

1. How does water colour affect the diet of perch and roach? (**III**)
2. Is water colour one of the factors regulating the interspecific interactions between perch and roach? (**III** & **IV**)
3. How does water colour affect growth and intraspecific interaction in perch populations? (**III–V**)

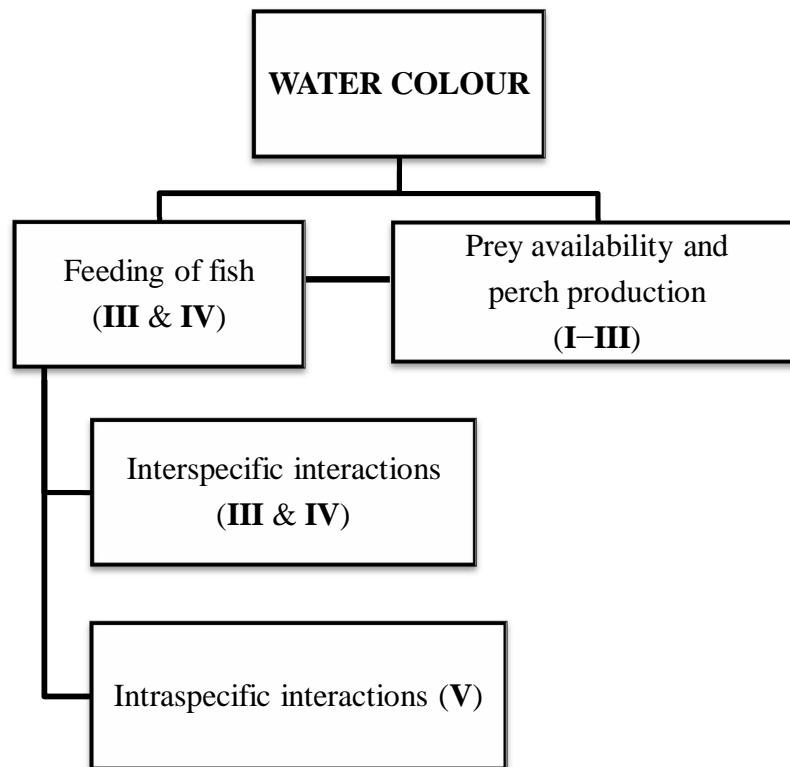


Figure 1. Schematic summary of the organization of the thesis.

The main hypotheses of the thesis are:

1. High water colour reduce the ability of fish to catch prey and strong thermal stratification in humic lakes restricts prey availability to fish
2. Effects of water colour on fish predation are species-dependent
3. Effects of water colour on perch predation are gender-dependent
4. The occurrence of the benthic bottleneck in perch growth is dependent on water colour

3. Materials and methods

3.1 Field studies

3.1.1 Study lakes

The study area is situated in the Evo district (61°13'N, 25° 12'E) in southern Finland. The study lakes Iso Valkjärvi, Hokajärvi, Haarakjärvi, Haukijärvi and Majajärvi are close to pristine and, other than scientific research, fishing is forbidden. The lakes are small and humic brown-water lakes typical of the temperate regions of Northern Europe. The surface area of the lakes varies between 2.1 and 13.8 ha, mean depth between 2.2 and 6.1 m, average total P concentration 8 and 22 $\mu\text{g l}^{-1}$, average total N concentration 440 and 700 $\mu\text{g l}^{-1}$ and water colour between 50 and 340 mg Pt l^{-1} (Table 1). All the study lakes are inhabited by perch, roach and pike; some have low abundances of other fish species (Olin et al. 2010). Samples for water quality (**I** & **II**) were taken fortnightly in 2006–2008 during the growing season (from May to September) (nine times per season). The gradient of dissolved oxygen (DO) concentration was measured with a YSI-6600 sonde (YSI Corp.) and light intensity with a LI-1400 datalogger with quantum sensors (**II**). The density (% coverage) of macrophytes (**I**) was estimated, using a 1-m² frame (five replicates), and the area of the macrophyte-covered littoral zone was measured using a global positioning system (GPS) device. Lake Iso Valkjärvi was not studied in papers **I** & **III**, but additional unpublished data on the lake are presented here to complement previous results (**I** & **III**).

Table I. Main characteristics and environmental variables of the lakes studied. Results of water quality values are average values (0–1 m depth) from May to September in 2006–2008.

	Iso Valkjärvi	Hokajärvi	Haarakjärvi	Haukijärvi	Majajärvi
Surface area (ha)	2.2	8.4	13.8	2.1	3.4
Mean depth (m)	3.8	2.2	6.1	3.8	4.6
Max depth (m)	8	6	12	8	12
Oxygenated area					
DO ₂ ≥ 2 mg l^{-1} (ha)	2.19	7.07	6.88	0.54	0.78
Water colour (mg Pt l^{-1})	50	130	150	330	340
Secchi depth (cm)	260	170	150	110	90
pH	5.7	6.3	6.1	6.0	5.7
Alkalinity (mmol l^{-1})	0.05	0.14	0.11	0.14	0.08
Tot-P ($\mu\text{g l}^{-1}$)	11	8	12	17	22
Tot-N ($\mu\text{g l}^{-1}$)	540	440	490	560	700
Chlorophyll a ($\mu\text{g l}^{-1}$)	9	3	6	7	11

3.1.2 Zooplankton and benthic macroinvertebrates

Zooplankton samples were taken every 2 weeks in 2006 during the summer with a tube sampler (height 40 cm, volume 2.5 l). To account for the spatial variability in zooplankton biomass (**I**), samples from the pelagic zone were taken from two different locations at the deepest part of each lake. From both locations, tube sampler hauls were conducted at 0–1, 1–2, and 2–3 m depths and assembled into one integrated sample. The study was targeted mainly at the epilimnetic zooplankton, but since water colour affects the vertical position and migration behaviour of zooplankton (Dodson 1990; Wissell & Ramcharan 2003), samples were also taken from the thermocline (five hauls) and hypolimnion (five hauls). From the littoral zone, samples were taken from four different sites among macrophyte stands (**I**). The planktonic crustaceans were enumerated and each species of cladocerans and copepods, 30 individuals were measured: *Daphnia* sp. from the centre of the eye to the base of the tail spine and other species from the anterior edge of the carapace to the posterior edge of the carapace (**I** & **III**). The zooplankton biomasses were calculated from individual lengths, using length-carbon regressions (Vasama & Kankaala 1990; Luokkanen 1995). The sampling for benthic macroinvertebrates (**III**) was conducted with a Kajak tube sampler (area = 54 cm²) both at the beginning and end of the growing season. The samples were taken from three parallel lines from the littoral zone to the deepest part of the lake. To estimate the density of partly planktonic prey (**III**), such as *Chaoborus flavicans* Meigen, over the bottom sediment, three replicate samples were taken with a 183 µm plankton net. Macroinvertebrates were picked out from samples and identified to species or genus, counted and weighted (wet mass/species). To estimate the abundance of benthic macroinvertebrates in oxygenated areas of the lake, the densities of benthic macroinvertebrates weighted to the oxygenated area (where DO was ≥ 2 mg l⁻¹ during the entire season) of the lake.

3.1.3 Fish sampling

Population parameters

The population size (**II**) of perch in each study lake was estimated by mark and recapture (Schnabel method) and the population size of pike by the Petersen-Chapman method (Krebs 1999). The population sizes were estimated annually during 2006–2008. Perch were captured with wire traps in spring (10–20 days after the ice break). Marking and recapturing of pike were conducted by wire traps and fyke nets in spring and by angling during a 1-week period in late August. Perch were marked by fin clipping and pike by Carlin or T-bar tags and fin clipping. From the mark-

recapture catch, sex and total length (TL, 1 cm length classes) were determined during marking and length distributions were calculated.

The relative abundance and size structure of roach and small perch were estimated annually by gillnetting three times in each lake in July–August with Nordic multimesh gillnets (Appelberg et al. 1995; Olin et al. 2004). The annual fishing effort per lake varied from 6 to 21 net nights. The exposure time of the nets was 12 h (overnight). Fish were counted, weighed (to the nearest gram) and measured (TL, 1 cm length classes) and catches per unit effort (CPUE) were calculated. The gender of each fish was determined (II & V) and perch growth at different ages was determined from the opercula and roach from scales. The ageing was verified from otoliths (perch) or cleithra (roach) (Horppila 2000). The back-calculated growth of perch was calculated for each individual with the Monastyrsky procedure (Bagenal & Tesch 1978), and Fraser-Lee equation (Fraser 1916; Lee 1920) was used to back-calculate the growth of roach (III).

Perch production estimates (II) were derived by (i) calculating sex-specific age-length keys, (ii) calculating the density (ind. ha⁻¹) of each sex and age class, using the sex- and length-specific density estimates and the age-length keys, (iii) multiplying the average yearly weight increment of each sex and age class by the density of the classes (e.g. Horppila & Peltonen 1994) and (iv) combining the sex- and age-specific production estimates as the total production estimate. The variances for the production estimates were calculated according to Newman & Martin (1983).

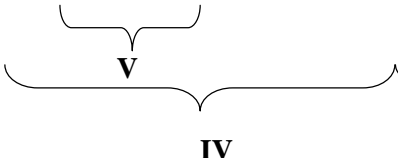
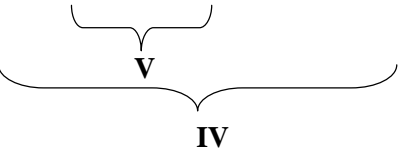
Fish diet

The diet data (n = 864 for perch and 569 for roach) were collected from the Nordic gillnet samples (III & IV). The stomach contents of perch were analysed (III & IV) for fullness and volume proportions of different food items (Windell 1971). Since roach lack a distinct stomach, the content of the anterior third of their gut was analysed (Vøllestad 1985; Rask 1989). For inter lake comparisons, different food items were pooled into three groups: zooplankton, benthic macroinvertebrates and fishes for perch, and zooplankton, benthic macroinvertebrates and plant material for roach. The electivity index by Ivlev (1961) was used as a measure of selectivity (E) for various zooplankton and macroinvertebrate taxa in fish rations: $E = (r_i - p_i) / (r_i + p_i)^{-1}$, where r_i = percentage of the food item in the ration, and p_i = % of food item in the environment. Food availability in the environment was calculated from samples taken on the same dates the fishes were sampled. The electivity index values of E range from -1.00 (complete avoidance) to +1.00 (exclusive selection). Zooplankton taxa were specified to species level and benthic macroinvertebrates to species or genus level.

3.2 Laboratory experiments – The role of water colour and competitive interactions

Perch and roach were used as planktivores in the experiments (IV). The fish were captured with wire traps (perch) and pound net (roach) from the highly humic Lake Majajärvi (Table 1). After capture, the fish were acclimatized under laboratory conditions for 2 weeks at 15 °C. The average TL of the perch ($\pm 95\%$ CL) was 10.0 ± 0.20 cm, weight 9.9 ± 0.7 g and age 2–3 years (IV & V). The average TL of the roach ($\pm 95\%$ CL) was 11.1 ± 0.13 cm and weight 11.2 ± 0.6 g (IV). The experiments were conducted in 1000 l plastic tanks filled with 15°C water. The water was filtered to the tanks through a 50 μm net to remove any food items from the water. The light levels above the water surface were adjusted to represent twilight conditions ($0.1 \mu\text{mol m}^{-2} \text{ l}^{-1}$) (LI-1400 data logger equipped with a LI-192SA quantum sensor). The fourth instar larvae (body length app. 10 mm) of *C. flavicans* used in the experiments as prey were collected with net hauls from Lake Majajärvi (IV & V). The prey density (one ind. l^{-1}) was adjusted to represent the typical density of *C. flavicans* in Lake Majajärvi (Valonen 2009). The experiments were conducted both in highly humic water (340 mg Pt l^{-1}) and clear water ($< 10 \text{ mg Pt l}^{-1}$). The basic fish assemblage (IV) was 3 perch to which were added 3, 6 or 9 perch (pure shoals) or roach (mixed shoals), the total experiment densities thus being 3, 6, 9 and 12 fish (Table 2). Three replicates of each treatment were conducted.

Table 2. Summary of the experimental design. Three replicates of each treatment were conducted (IV & V).

Clear water		Dark water	
Pure shoals (Perch)	Mixed shoals (Perch + Roach)	Pure shoals (Perch)	Mixed shoals (Perch + Roach)
3	–	3	–
6	3 + 3	6	3 + 3
9	3 + 6	9	3 + 6
12	3 + 9	12	3 + 9
			

After starvation for 2 days, the fish were moved to experimental tanks and were left to acclimatize for 6 h before the trials. At the beginning of each trial, 1000 individuals of *C. flavicans* were released into the tanks. The short duration time of the trials (20 min) was set according to preliminary experiments to ensure that the prey density would be sufficient for all fish densities used (3, 6, 9 and 12), thereby not all prey individuals would be consumed during the trials at any fish density. After each experiment, the fish were captured with a small net and immediately killed by cutting the neck and weighed to the nearest milligram (mg), measured to the nearest mm (TL), after which the digestive tracts were removed. The prey items ingested (*C. flavicans* head capsules) were counted under a microscope from the mouth, pharynxes and stomach (perch) or intestine (roach).

To determine whether the effects of decreasing water transparency and increasing fish density on the feeding rate of planktivorous fish are gender-dependent, the gender of each perch was also determined (V). For this purpose, only the data on pure perch shoals were analysed (Table 2) (V). No differences in length ($F_{1,179} = 0.55$, $P = 0.4607$), weight ($F_{1,179} = 0.01$, $P = 0.9870$) or length-weight relationship ($F_{1,179} = 0.31$, $P = 0.5789$) were observed between male and female perch used in the experiments. Male and female perch were randomly distributed to the various experiments, since the gender of each fish was determined after the experiments (V). Of the 180 fish used in the experiments, 43% were males and 57% females.

3.3 Statistical analyses

The littoral and pelagic biomasses of the various crustacean zooplankton taxa in each lake and the inter lake differences in macrophyte coverage were compared with analysis of variance for repeated measurements (ANOVAR) (I). Pairwise comparisons in the inter lake analyses were performed with Bonferroni *t*-tests (I & III). The relationship between macrophyte coverage and littoral zooplankton biomass in each lake was studied with linear regression. The inter lake differences in mean body length of littoral and pelagic cladocerans were tested with analysis of variance (ANOVA), and the dependence of cladoceran mean length on Secchi depth within each lake was determined with linear regression (I & III). Pair wise comparisons in the inter lake differences in abundance of benthic macroinvertebrates were performed with Bonferroni *t*-tests. The inter lake differences in the benthic macroinvertebrate species composition were tested with ANOVA (III).

The inter lake differences in the annual growth increments of perch (**II**, **III** & **V**) and roach (**III**) were tested with ANOVA including Bonferroni correction (Horppila & Nyberg 1999). The effects of water quality parameters, as well as roach and perch abundance, on the perch population parameters were determined with regression analysis, using the estimated mean values of dependent and independent variables (**II**). When necessary, the datasets were $\ln(x + 1)$ -transformed to improve normality (**II**).

The effect of Secchi disc depth on the selectivity of perch and roach for daphnids in the study lakes was tested with linear regression (**III**). The inter lake differences in the niche-shift length of perch (the mean length when $\geq 50\%$ of stomach the contents consisted of zooplankton, macroinvertebrates or fishes) were tested with ANOVA. Pair wise comparisons in the inter lake differences were performed with Bonferroni *t*-tests (**III**).

A logistic regression model (**IV**) was used to analyse the proportion of perch utilizing zooplankton as a function of perch length (L) following Tolonen et al. (1999): $y = \exp(\alpha + \beta L + \gamma C + \delta LC) / [1 + \exp(\alpha + \beta L + \gamma C + \delta LC)]^{-1}$, where y is the occurrence of a food category or item in a single fish recorded as 0 (does not occur) or 1 (does occur), L = length, C = water colour and β , γ and δ are parameters and α = constant variable. This model was used to test whether the utilization of zooplankton was dependent on perch length, and if there were an interaction with perch length and water colour. The fit of the logistic regression model was estimated with the likelihood-ratio test.

The effects of water colour, fish species and density of fish on perch and roach predation rates were tested with analysis of covariance (ANCOVA) using the fish density as a covariate (**IV**). The effects of water colour and perch density on the feeding rates of male and female perch in the experiments were studied with two-factor ANOVA (**V**). In the field data, the female-male difference in the average annual length increment was calculated for each lake for age groups 1–6 and plotted against the water colour of the lakes. The effects of water colour on the female-male differences in annual length increments were determined with linear regression analysis (**V**).

4. Results

4.1 Environmental variables

The surface water temperature in the study lakes increased from 11 °C to 13 °C in May to 25–26 °C in July, being 0.5–1.0 °C higher in the more humic lakes (Haukijärvi and Majajärvi). All five lakes were stratified during summer and the concentration of DO was low ($<2 \text{ mg l}^{-1}$) in the hypolimnion. The thickness of the oxygenated water layer varied from 3.0 m (Majajärvi) to 11.7 m (Haarajärvi). The average Secchi depth varied from 90 cm to 260 cm and water colour from 50 to 340 mg Pt l^{-1} . The percentage of the littoral zone of the total lake area, varied between 4% and 27% of the lake area, being highest in Lake Hokajärvi (I). In all the lakes, floating-leaved macrophytes (mainly yellow water-lily *Nuphar lutea* (L.) Sim.) formed the largest stands, and belts of the emergent species (mainly common reed *Phragmites australis* (Cav.) Trin. ex Steudel) were also commonly observed. The density of the submerged macrophytes was low in all the lakes.

4.2 Prey availability

The zooplankton biomass was higher in the littoral zone than in the pelagic zone only in Hokajärvi, which had the highest water transparency among the study lakes (I, Iso Valkjärvi was not included in this study). Variations in the length distributions of cladocerans emphasized the refuge effect of the littoral zone in lakes with higher transparency, and in contrast the protective effect of highly coloured water (Fig. 2).

The average size of cladocerans in the pelagic zone decreased significantly ($P = 0.0106$) with Secchi depth of the lake (I). In addition, the mean cladoceran size in the two clearest lakes was higher in the littoral than in the pelagic zone, whereas in the other two lakes with lower transparency a contrasting situation was found. Moreover, in the pelagic zones of Haarajärvi and Haukijärvi, the average size of cladocerans decreased steeply when the water transparency showed a peak (I).

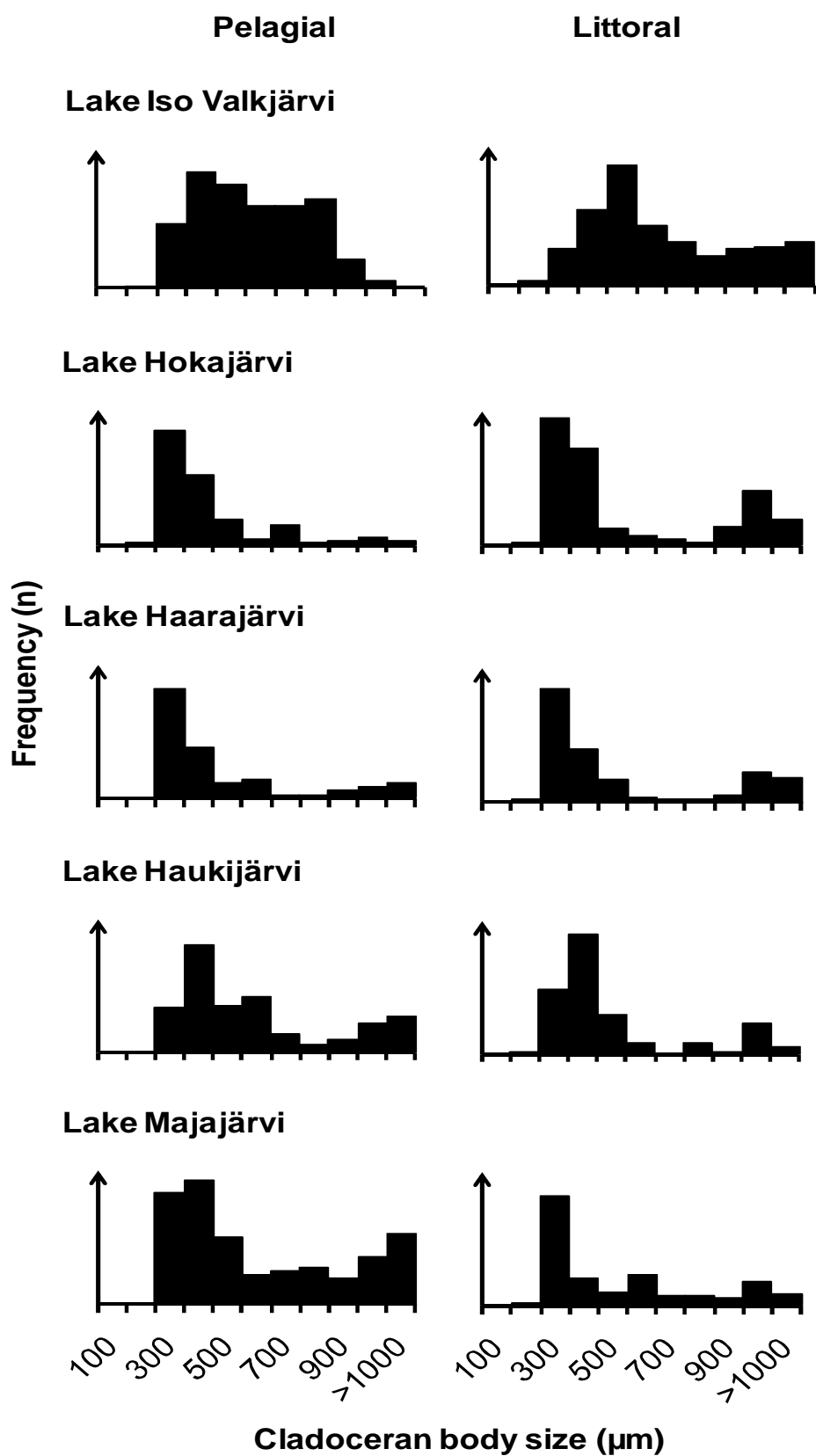


Figure 2. Length distributions of cladocerans in pelagic and littoral zones in the lakes studied. The lakes are in order of increasing water colour from top to bottom (I, modified; Lake Iso Valkjärvi, unpublished data).

The abundance of benthic macroinvertebrates in the lake area with DO concentration $>2 \text{ mg l}^{-1}$ were higher in the less humic lakes (III) (Fig. 3). Chironomids and chaoborids comprised 70–90% of the benthic invertebrate density in all lakes studied (III). There were no significant differences in benthic macroinvertebrate species composition between lakes, but large-sized species, such as trichopterans and ephemeropterans, were more abundant in less humic lakes (III).

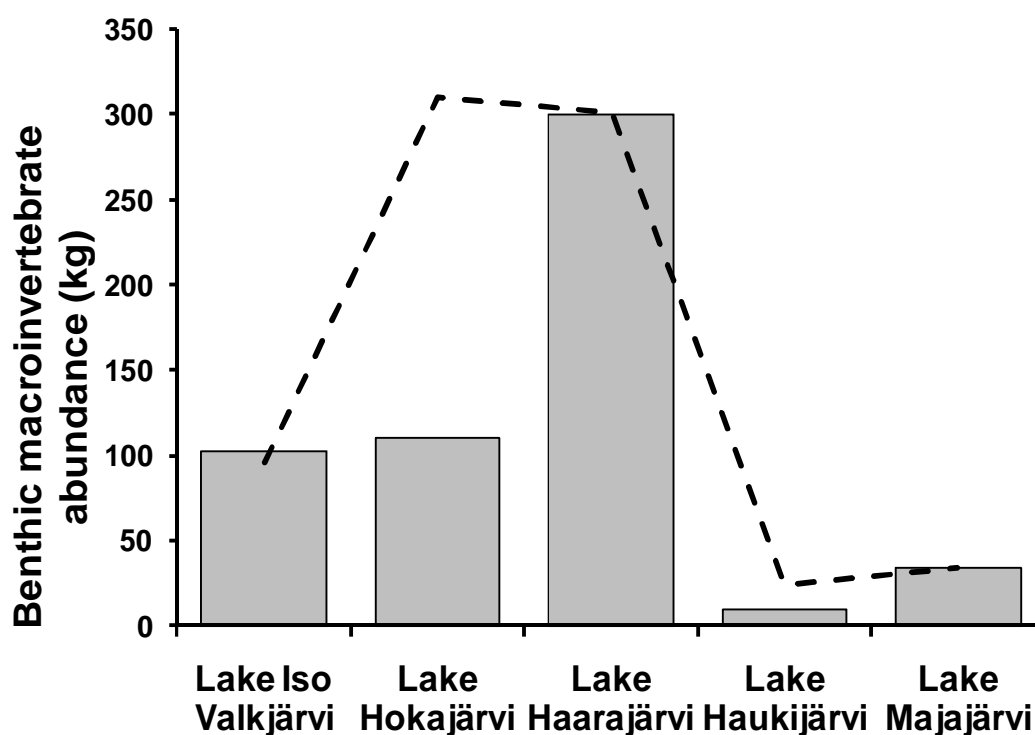


Figure 3. Total biomass of benthic macroinvertebrates in the oxygenated ($>2 \text{ mg O}_2 \text{ l}^{-1}$) bottom areas of the study lakes (III, modified; Lake Iso Valkjärvi unpublished data). Dashed line describes the oxygenated area of the lake.

4.3 Fish density and growth

The densest perch populations were recorded in the clearest lake (Iso Valkjärvi) and darkest (Majajärvi), where the average perch densities in 2006–2008 were 1360 and 2600 ind. ha^{-1} . In Hokajärvi, Haarajärvi and Haukijärvi, the average density estimates were 750, 950 and 1310 ind. ha^{-1} , respectively (Table 3). The average perch biomass was 44, 46, 23, 15, 13 kg ha^{-1} in Iso Valkjärvi, Majajärvi, Haukijärvi, Haarajärvi and Hokajärvi, respectively (Table 3).

The highest average gillnet catch of roach (475 g net⁻¹) was recorded in Haukijärvi, whereas the highest catch in numbers (43 fish net⁻¹) occurred in Haarajärvi (Table 3).

Clearly, the lowest roach catches both in biomass and in numbers were recorded in Iso Valkjärvi, where roach were practically absent (Table 3). The density of pike was highest in Haarajärvi and Majajärvi (22 ind. ha⁻¹) and lowest in Iso Valkjärvi (3 ind. ha⁻¹). The highest biomass of pike (13 kg ha⁻¹) was recorded in Majajärvi (Table 3).

Table 3. Density and biomass estimates of perch and pike and the gillnet CPUE of roach in the study lakes.

	Perch density ind. ha ⁻¹	Perch biomass kg ha ⁻¹	Roach CPUE ind. net ⁻¹	Roach CPUE g net ⁻¹	Pike density ind.ha ⁻¹	Pike biomass kg ha ⁻¹
Iso Valkjärvi	1360	44	0.2	92	3	3
Hokajärvi	750	13	20	362	19	10
Haarajärvi	950	15	43	408	22	11
Haukijärvi	1310	23	28	475	11	12
Majajärvi	2600	46	12	217	23	13

The back-calculated data showed that the growth rates of perch and roach were relatively slow in the lakes studied (Fig. 4). The slowest growth rate of young perch was observed in the darkest lake (Majajärvi), where the average length of 1-year-old perch was 50 mm, and the fastest in the clearest lake (Iso Valkjärvi), where the average length was 61 mm (Fig. 4). The most pronounced inter lake differences in the growth of young perch were detected in the second year, when the length increment in Iso Valkjärvi (34 mm) was significantly higher than in any of the other lakes (ANOVAR, $P < 0.0001$). The inter lake variations in growth were smallest at 4–5 years of age (Fig. 4), but at 6 years of age, the growth differences increased again, the length increments of perch being higher in Haarajärvi (24 mm) and Hokajärvi (19 mm) than in the other lakes (Fig. 4).

The only significant difference in growth rates of roach (ANOVAR, $P > 0.001$) was detected between Haarajärvi and the other lakes in the second year (Fig. 4).

Due to the constantly slow growth rate of roach in Haarakjärvi, the length of roach was on average lower than in the other lakes (Fig. 4).

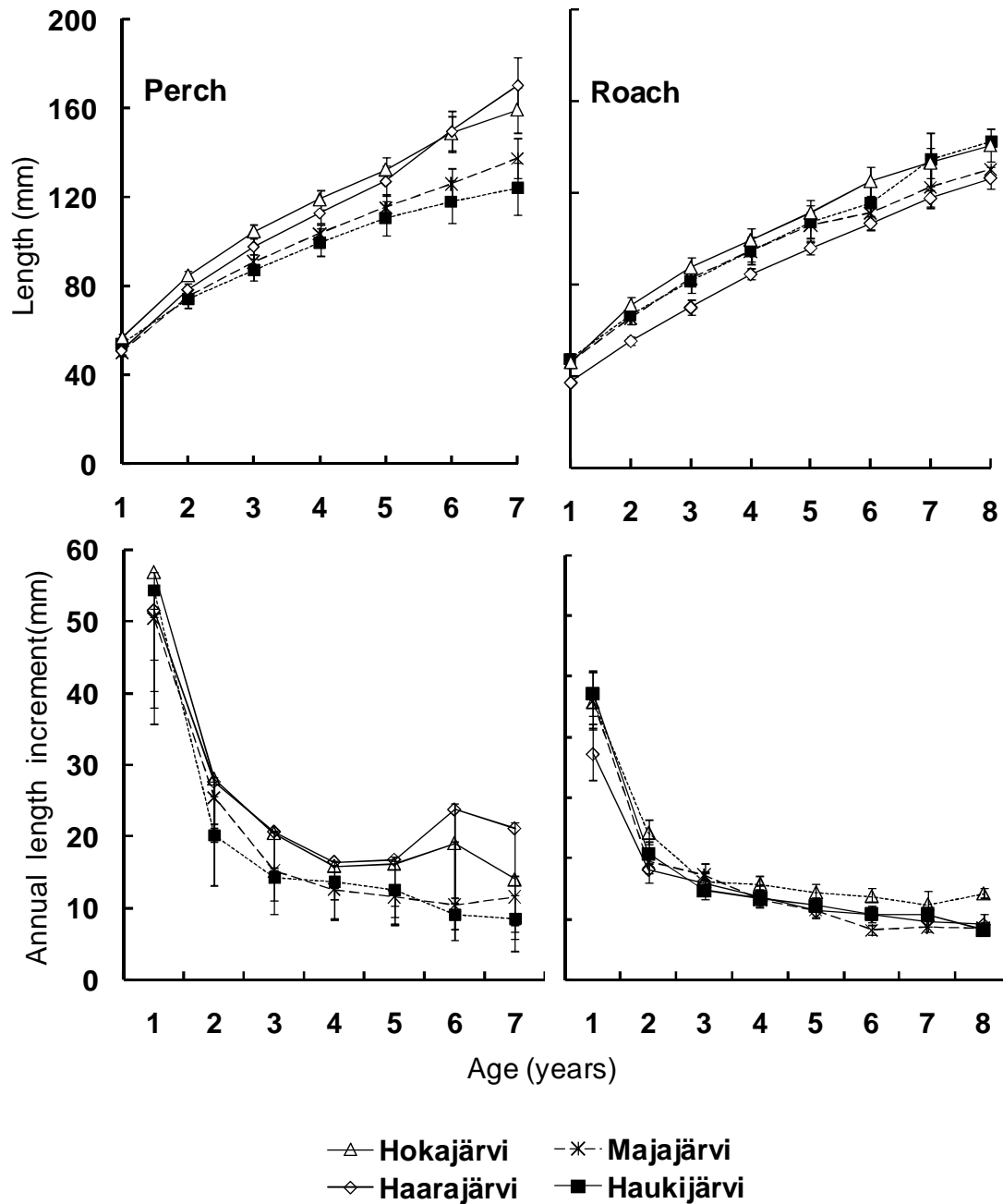


Figure 4. Average annual length increments (top) and average length at age (\pm 95% confidence limits) (bottom) of perch (left) and roach (right) in the study lakes.

4.4 Perch production and water quality effects on perch population parameters

Perch production was clearly highest in Majajärvi, where the average annual production during the three study years was 16.5 kg ha⁻¹. The inter year variation in the estimates was high, with production ranging from 7.3 kg ha⁻¹ to 24.6 kg ha⁻¹. In the other four lakes, the annual variations were much smaller. The average production estimates in Iso Valkjärvi, Haukijärvi, Hokajärvi and Haarajärvi were 6.7, 6.0, 6.0 and 9.8 kg ha⁻¹, respectively.

Perch density was significantly correlated with total P concentration of the lake ($r^2=0.832$, $P=0.0310$). Perch production was independent of total P concentration, which was due to the low production in Haukijärvi. When Haukijärvi was excluded from the regression analysis, the total P concentration strongly affected on perch production ($r^2=0.955$, $P=0.0226$). The length increment of perch in their second year was significantly correlated with Secchi depth ($r^2=0.781$, $P=0.0469$), but at older ages (≥ 3 years), the annual length increments showed no relationship with Secchi depth.

Perch density, biomass and production showed no relationship with the oxygenated water layer. No effect of pH on perch production or density was found, but perch biomass decreased significantly with increasing pH ($r^2=0.927$, $P=0.0087$).

4.5 Fish diet in humic lakes

Water colour had a strong relationship with the prey selection and diet shift length of perch. The Secchi disc depth positively affected the selectivity of planktivorous perch on daphnids ($r^2=0.790$, $P<0.05$) (III). In the less humic lakes (Hokajärvi and Haarajärvi), perch selected more for macrophyte-associated macroinvertebrates, such as odonates, than in more humic lakes (III).

Roach favoured *Bosmina* Baird sp. and also larger cladocerans (daphnids) in their diet, regardless of Secchi disc depth. On average, the benthic diet of roach was similar in all the lakes studied (III). Unlike perch, roach did not feed on macrophyte-associated species.

The primary plankton feeding phase of perch was significantly longer (ANOVA, $P>0.05$) in less humic lakes (Hokajärvi and Haarajärvi) (Fig. 5) (III). A pronounced trend between water colour and perch shift to benthivory was detected: the higher the water colour the earlier that perch shifted to feed mainly on macroinvertebrates (Fig. 5) (III). Logistic regression analysis showed (IV) that the probability of perch shifting from primary plankton feeding to other food resources was also dependent on perch length and water colour (see Discussion Fig. 9). In less humic lakes (Hokajärvi and Haarajärvi), the benthic macroinvertebrate phase was relatively short and perch shifted to piscivory at lengths of > 130 mm (Fig. 5) (III).

In the more humic lakes (Majajärvi and Haukijärvi), perch already shifted to macroinvertebrate diets at lengths of >100 mm and did not clearly shift to piscivory at any length (Fig. 5) (III).

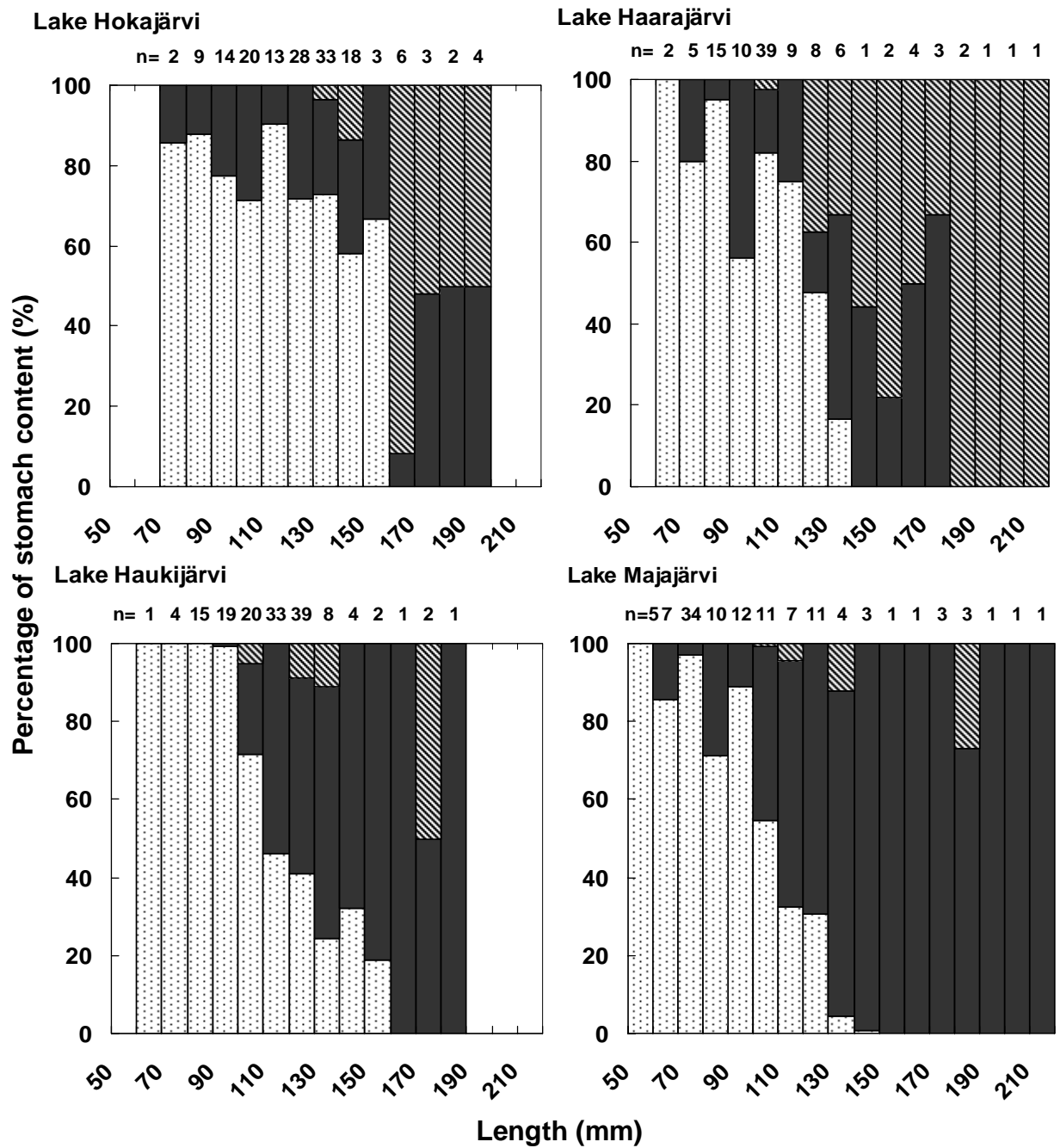





Figure 5. Percentage composition of food items (zooplankton , benthic macroinvertebrates  and fish ) in stomach contents (mean values from three sampling dates) in relation to perch size in the lakes studied. Lakes are in order of increasing water colour from left to right (III).

The diet shifts of roach were similar in the study lakes, with the exception of the less humic Lake Haarakjärvi, where roach shifted to benthic macroinvertebrates and plant material earlier (Fig. 6) (III). At lengths of < 100 mm, roach fed mainly on zooplankton and gradually shifted to feed on a mixture of zooplankton, benthic macroinvertebrates, algae and plant material in all the lakes (Fig. 6).

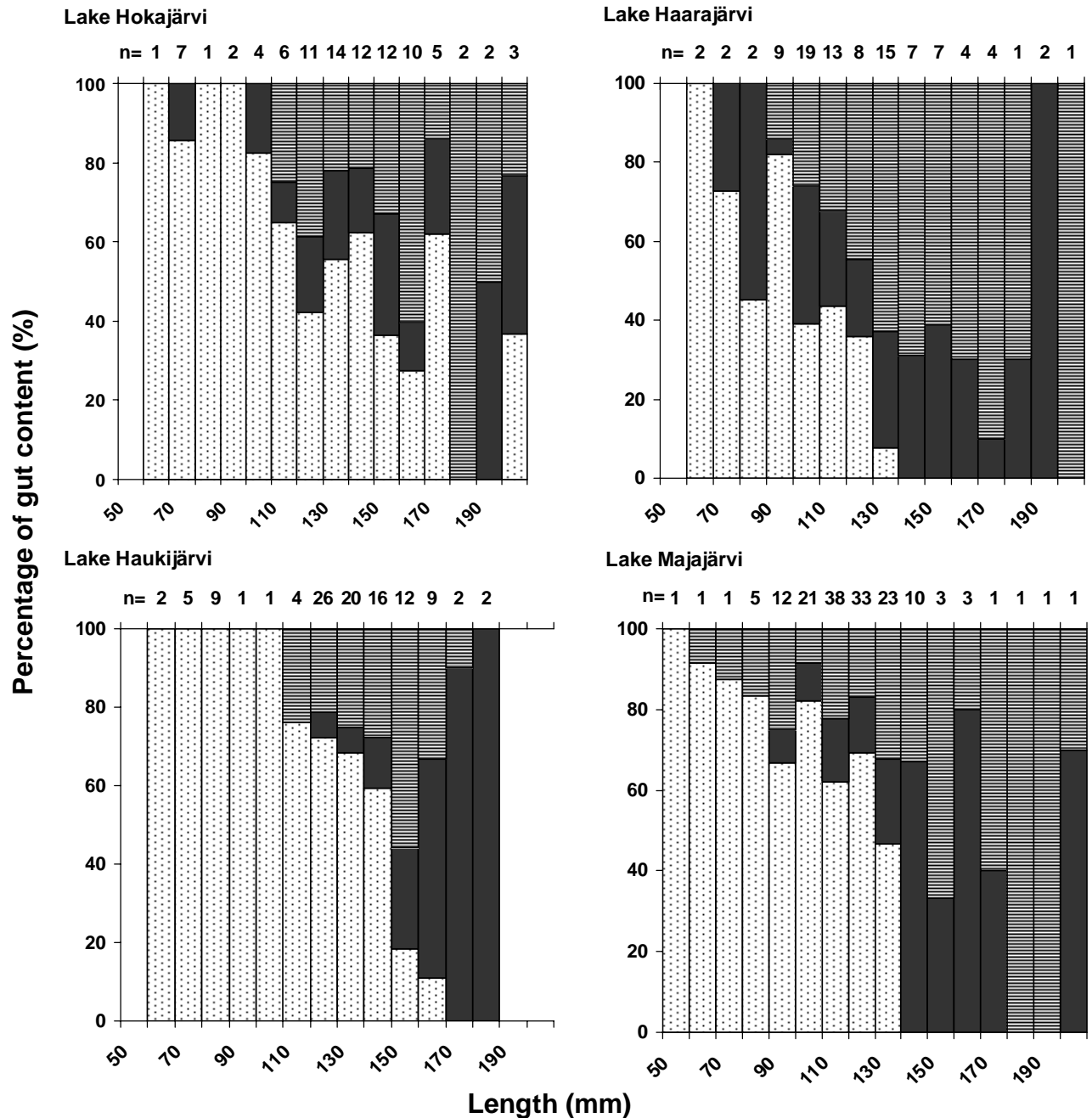





Figure 6. Percentage composition of food items (zooplankton , benthic macroinvertebrates , and plant material ) in gut contents of roach in the lakes studied (mean values from three sampling dates). Lakes are in order of increasing water colour from left to right (III).

4.6 Water colour and interspecific competition

Feeding of perch was severely disturbed by the high water colour in the experiments (Fig. 7) (IV). The presence of roach had no significant effect on the feeding rate of perch ($P = 0.372$). Perch in pure perch shoals fed slightly more effectively on *C. flavicans* larvae than perch in mixed shoals, but only in clear-water trials (Fig. 7) (IV). There was no significant change in the feeding efficiency of perch when fish density was increased (Fig. 7). The increase in roach density had a slightly negative, but non-significant effect on the feeding efficiency of perch in clear-water trials, but not in the highly humic water trials where the overall feeding efficiency was quite low (Fig. 7) (IV).

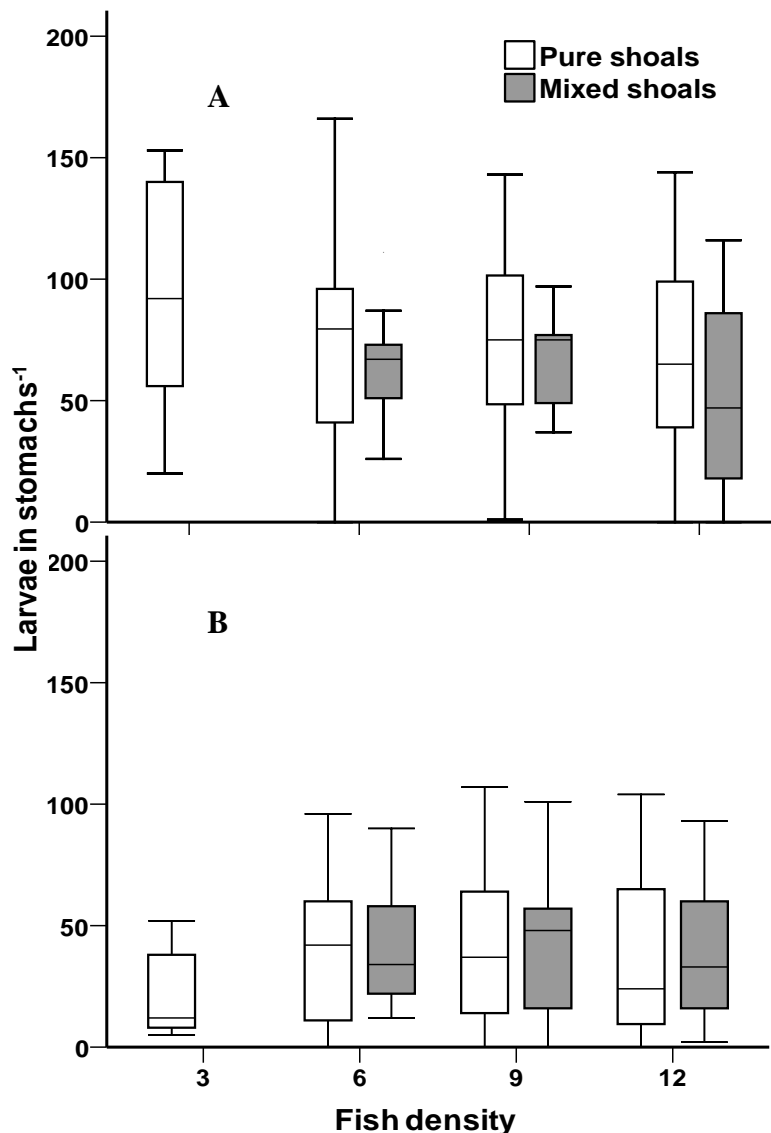


Figure 7. Effect of increasing fish densities on perch consumption of *C. flavicans* (larvae fish⁻¹) in perch shoals and in mixed shoals with roach in clear-water (A) and highly humic water (B) experiments (IV).

4.7 Water colour and intraspecific competition

When all the various treatments (water colour and perch densities from 3 to 12) were pooled, the average feeding rate of females was higher but not significantly different from that of male perch (V). However, the feeding of female perch decreased more in humic water trials than that of males (Fig. 8). In the statistical analysis, the gender-water colour interaction was highly significant ($P = 0.0004$) (V), confirming that the effect of water colour on the feeding rate was gender-dependent.

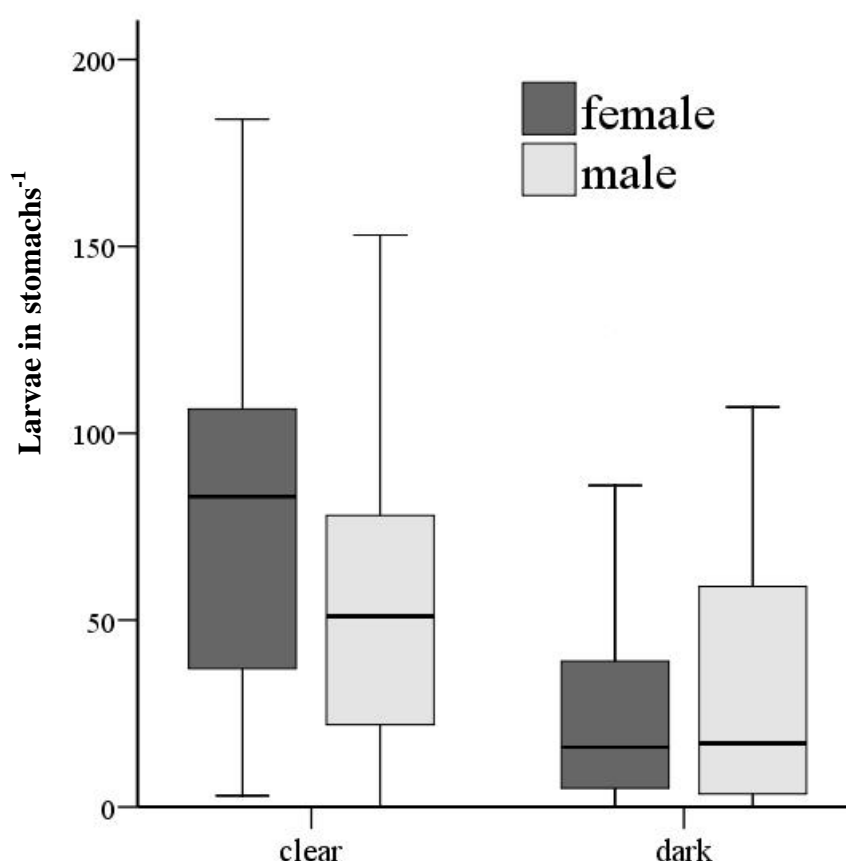


Figure 8. Average number of *Chaoborus flavicans* larvae consumed by female and male perch in the experiments (V, modified).

The experimental results were supported by field data, that revealed a significant effect of water colour on the gender growth difference in planktivorous 3-year-old perch (V). This was expected because in the study lakes this is the only age group of perch that is fully mature, but still largely dependent on zooplankton.

5. Discussion

5.1 Water colour and prey availability

The zooplankton results (**I**) supported previous findings that emergent and floating-leaved macrophyte species may be of importance in protecting zooplankton from fish predation in lakes where submerged species are sparse, due to light limitation (Nurminen & Horppila 2002; Nurminen et al. 2007; Cazzanelli et al. 2008). Since the littoral zooplankton biomass followed the macrophyte biomass only in the less humic lakes, the high water colour may have compensated for the macrophytes as a refuge for zooplankton against fish predation in more humic lakes (Haukijärvi and Majajärvi). The cladoceran length distributions showed a trend toward greater water clarity in the study lakes. In the pelagic zones, the large-sized cladocerans were scarce in the less humic lakes, but relatively common in the more humic lakes (Haukijärvi and Majajärvi). Large-sized cladocerans were more common in the littoral than in the pelagic zones of the three clearest lakes, indicating a possible refuge effect of macrophytes. In the clearest lake (Iso Valkjärvi), the cladoceran length distribution interestingly differed from that in other lakes. The proportion of medium-sized (500–800 μm) cladocerans was higher than in other lakes, possibly due to the lack of roach predation in Iso Valkjärvi, where roach were practically absent. Mean cladoceran size was associated with water colour, indicating that the feeding efficiency of planktivorous fish increased with increasing water clarity (Soranno et al. 1993; Wissel et al. 2003).

The benthic macroinvertebrate densities per metre squared varied among the lakes, regardless of water colour, but in taking into account the areas with DO concentration $> 2 \text{ mg l}^{-1}$, the total benthic macroinvertebrate abundances were lower in the highly humic lakes, due to smaller oxygenated areas. In addition, when the amount of benthic macroinvertebrates (kg per lake) was divided with the perch biomass (kg per lake), there were 1.0–1.4 kg benthic macroinvertebrates per perch kg in the three clearest lakes, but only 0.2 kg benthic macroinvertebrates per perch kg in lakes Haukijärvi and Majajärvi (unpubl.). The thickness of the oxygenated water layer may therefore be an important factor limiting the foraging possibilities of fish in strongly stratifying humic lakes (Rask et al. 1999).

5.2 Associations between water colour and perch production

Abiotic factors, such as nutrient supply and light energy, commonly set limits on fish production in lakes, but actual productivity is determined by the food web structure, which again is dependent on interspecific interactions (Carpenter et al. 1987). The main factor behind the inter lake differences in perch production in the study lakes was the fish density, rather than individual growth rate. In the study lakes, the nutrient supply (expressed as total P concentration) regulated the fish density and

probably also the recruitment (**II**). With increasing concentration of P, the biomass of zooplankton and zoobenthos in lakes usually increases (Hanson & Peters 1984), creating a higher potential for fish recruitment and production.

Water colour had a stronger effect on individual growth than on fish density. The growth rate of perch during the second year of life was dependent on water transparency (cf. Heibo et al. 2005), being slowest in the more humic lakes (Majajärvi and Haukijärvi). The rapid growth of young planktivorous perch in the clearest lake (Iso Valkjärvi) was probably due to the successive feeding efficiency of zooplankton. While the growth rate of young perch was dependent on water colour, the growth rate of older individuals was regulated by perch density (**II**). This change in the regulatory factors during fish growth was explained by the changing feeding habits of perch during their ontogeny.

5.3 Water colour effects on perch diet

The differences in the growth rate of perch during the second year of life could be explained by their diet. Zooplankton predominated in the diets of small perch in the study lakes (**III**), but the shift to benthivory occurred earlier in darker lakes. Persson and Greenberg (1990) showed that juvenile perch shift earlier and at a smaller size to feeding on benthic macroinvertebrates if zooplankton resources are severely limited, e.g. by density-dependent interactions such as competition. The high competition for zooplankton resources was probably not the ultimate reason for the earlier shift by perch from planktivory in the study lakes, because the crustacean zooplankton resources were most plentiful in the darkest lake (Majajärvi) where perch shifted at the smallest size to benthivory. There was also a significant positive relation between cladoceran mean size and water colour (**I**). Accordingly, perch feeding was severely disturbed by the high water colour in the experiments (**IV** & **V**). Therefore, it is conceivable that the high water colour probably hampered the vision of planktivorous perch through reduction in zooplanktonic prey detection and forced the perch to focus on macroinvertebrate prey, since benthic feeding is less visually oriented (Crowl 1989).

When perch shifted to feeding on benthic macroinvertebrates in the study lakes, the effect of perch density on perch growth was strongest. It is likely that intraspecific competition for benthic food restricted the growth rate of perch (benthic bottleneck, Persson & Greenberg 1990). In the more humic lakes, the coverage of the oxygenated littoral area was particularly narrow, which most likely limited the availability of benthic macroinvertebrates, confined perch benthivory to a smaller area and increased intraspecific competition for benthic food. As a result, perch recruitment to piscivory was delayed in the more humic lakes (Fig. 9). In the less humic lakes, the perch turned to piscivory through a relatively short macroinvertebrate phase (Fig. 9), but continued feeding on benthic

macroinvertebrates in darker lakes, which likely again increased competition for benthic food resources between different age classes in the perch population (Fig. 9). The results also support the findings of Radke and Gaupisch (2005) that low visibility may be a major factor suppressing the shift from feeding on macroinvertebrates to foraging on fish, because perch capture success decreased significantly along with decreased visibility. Additionally, Heibo et al. (2005) reported that under unfavourable conditions the second niche shift from benthivory to piscivory may not occur and as a result perch growth decelerates.

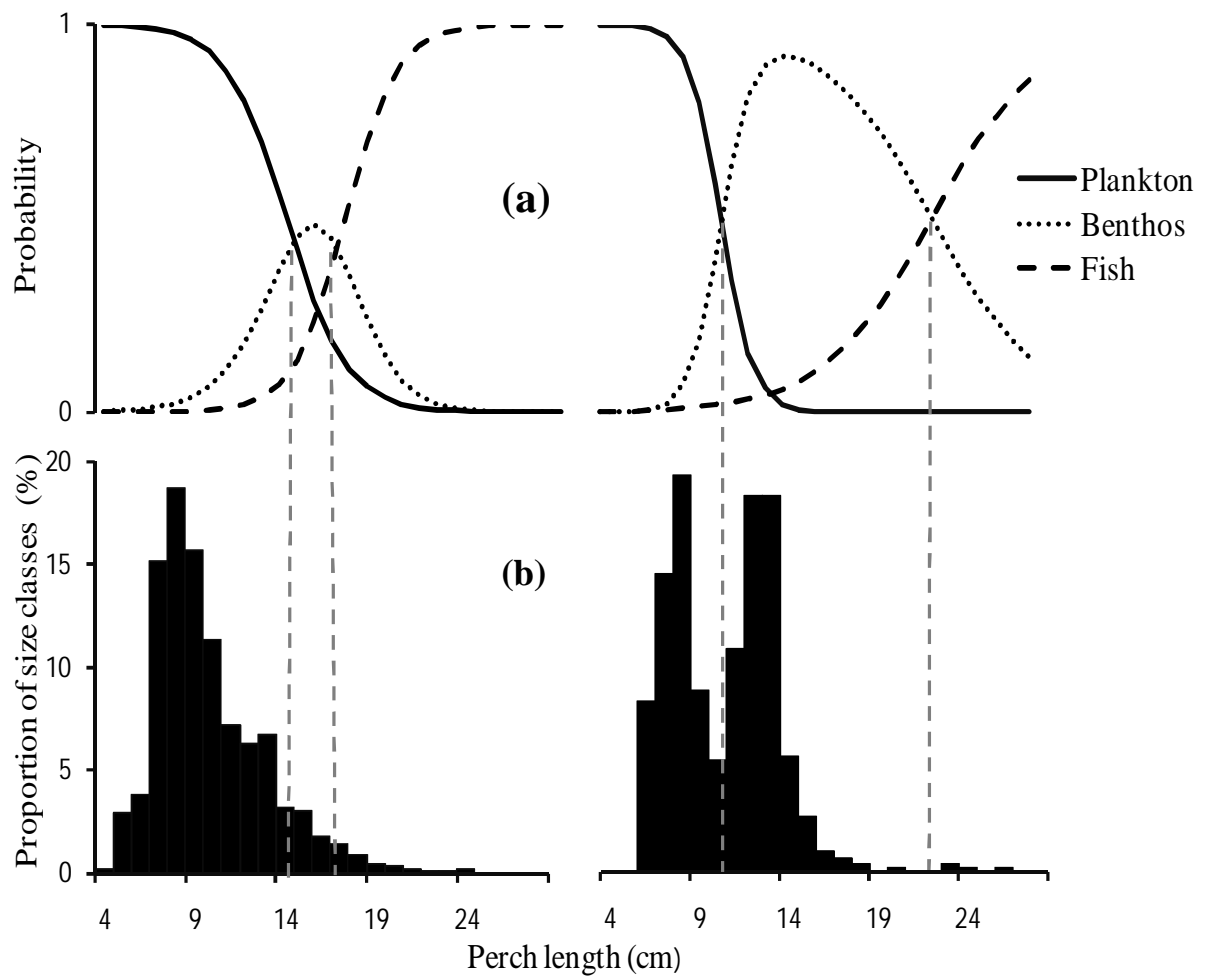


Figure 9. Probability of perch diet shifts against perch length estimated with logistic regressions (a) in less humic lakes ($< 140 \text{ mg Pt l}^{-1}$) (left) and more humic lakes ($> 300 \text{ mg Pt l}^{-1}$) (right) and the perch population length distribution (b) in the lakes at issue. The vertical dashed lines describe the size interval in the perch population wherein the benthic feeding of the perch phase is predominant and the suggested interspecific competition the strongest.

The growth rate of roach was also relatively slow in the study lakes, indicating restricted food resources (Rask et al. 1999). There were no significant differences in growth rates or diets of roach between lakes, with the exception of Lake Haarajärvi, where the growth of roach was slightly slower and fish density highest. In Haarajärvi, roach fed less on zooplankton and more on plant material than in other lakes. Since the nutritional value of plant material is lower than that of animal food, the high proportion of plant food may indicate competition for food resources (Persson 1983). In contrast to perch, the feeding efficiency or prey selectivity of roach was not affected by water colour.

Some studies have shown that perch are active at low light intensities, while increased turbidity and low levels of illumination in the water may act as compensatory factors on reduced feeding of perch (Craig 1987; Granqvist & Mattila 2004). Granqvist and Mattila (2004) suggested that low water transparency could offer protection to young perch from predators, which could lead to reduced cover-seeking behaviour and hence to increased feeding activity. However, most of the perch foraging experiment studies (Persson 1985; Diehl 1988; Granqvist & Mattila 2004; Snickars et al. 2004) were conducted in quite small experimental units (30–300 l), which would have increased predator-prey encounter rate and caused errors in the results. In the study lakes, the predation threat for perch comes mainly from pike and large perch. However, the effect of pike predation on perch is complex, because pike predation may reduce intraspecific competition in perch populations by cutting down the perch population and therefore individual perch would grow faster (Persson et al. 1996). In addition, Berg et al. (1997) found that pike impacted more the roach than the perch density, thus reducing the competition of these species. The effect of predation threat on perch behaviour also needs further investigation (IV).

Factors affecting habitat distribution, resource partitioning, diet selection and the timing of ontogenic niche shifts may be numerous. The study lakes vary in morphometry, productivity, availability of resources, biomass of planktivores and piscivores and littoral habitats. However, humic lakes are relatively stable systems with regard to water quality (Wetzel 2001) and the year-to-year timing of diet shifts is quite consistent in the study lakes. Olin et al. (2010) studied the effects of several abiotic and biotic factors on various population parameters of perch in humic lakes, including the study lakes, and suggested that perch populations are affected by biotic factors such as interspecific competition by roach and predation by pike, but the intensity of the interactions are regulated by abiotic factors, such as lake size and general productivity, with water colour as one of the most important single factors.

5.4 Water colour effects on interspecific interactions

Perch early niche shifting from planktivory to benthivory may result from increased interspecific competition with roach (Persson & Greenberg 1990), which may eventually cause a bottleneck in perch growth. Persson (1987) suggested that the competitive interaction of the species may be asymmetric and favour roach. Persson and Greenberg (1990) showed that roach are more efficient plankton feeders than perch. However, in clear-water experiments, perch were superior planktivores compared with roach.

The presence of roach may also reflect a behavioural response by perch, decreasing perch movement in clear water (pers. obs.). This slightly negative, but nonsignificant, effect of increasing roach density was detectable only in clear-water experiments when perch feeding would otherwise be optimal. Furthermore, no significant relationship between total fish or roach abundance and perch niche shift length were found in the field data (**III** & **IV**). Variability in water colour was probably also a reason why no significant effect of roach on the growth of small perch was detected. However, at the age of 7 years, the growth of perch increased with increasing roach abundance (**II**), suggesting that roach served as a resource for piscivorous perch in less humic lakes.

Water colour may have both direct and indirect effects on interspecific interaction of perch and roach. Compared with roach, perch may be inferior foragers on zooplankton in highly coloured water. As an indirect effect, water colour decreases the coverage of macrophytes and oxygenated littoral area that limits suitable, perch favoured littoral habitats (Diehl 1988) whereas roach are more efficient planktivores in simple-structured (Persson 1987) turbid or coloured waters (Nurminen et al. 2010).

5.5 Water colour effects on intraspecific interactions

Earlier shifts from planktivory in highly coloured lakes most likely increased intraspecific competition in perch populations. Moreover, the exiguous amount of benthic prey in the two darkest lakes probably tightened up the already high competition for food resources. Interestingly, the results also indicated that variations in visibility may regulate sexual dimorphism through divergent effects on the prey capture rate of males and females. In many fish species, the success of reproduction correlates positively with the size of females, while the size of males is less important (Trippel & Neilson 1992; Chambers & Leggett 1996). This also holds for perch (Craig 1987; Heyer et al. 2001) and it could thus be expected that females have a higher demand for food acquisition than males. Since female perch have higher demands for growth, the negative effect of water colour focused on their feeding and males were less affected.

Males and females may have variable strategies for tradeoffs between predation threat and food acquisition, due to the varying demands for energy acquisition (Holtby & Healey 1990, Mooring et al. 2003). Rennie et al. (2008) and Roff (1983) suggested that the slower growth rate of males could be explained by decreased feeding activity to reduce predation risk. Males showed lower feeding rate in clear-water experiments, where the danger of being detected by predators is much higher than in humic water. There were no predators present in the experiments, but the water to the tanks was taken from natural environments where piscivores (pike and predatory perch) are present, and chemical cues from predatory fish such as pike affect the behaviour of prey fish (Mathis et al. 1996).

The experiments were conducted in early summer, approximately four weeks after the spawning period, and it can be assumed that the results represented a period in which the differences between male and female perch were small. Later in the growing season, when the gonads again begin to develop and the demand for energy acquisition of perch females rises more steeply than that of males (Henderson et al. 2000), the response difference of the genders to water colour variations could be larger than in the present experiments.

The results of experiments and field data (V) support the findings of Fontaine et al. (1997) that variations in feeding rate may lead to sexual growth dimorphism in perch. Large females are known to play a key role in maintenance of populations and resource stocks in fisheries (Berkeley et al. 2004). Birkeland and Dayton (2005) concluded that generally large females produce high amounts of better-surviving larvae and contribute highly to reproduction. Therefore, based on the results of the experiments and field studies, high levels of water colour may have cascading effects on perch population dynamics and community structures.

6. Conclusions

High levels of water colour and strong thermal stratification in humic lakes can enhance refuges where prey can avoid fish. Water colour has different effects on species, depending on species-specific life-history traits and trophic interactions. Fish species whose success in predation is based on visual cues are more susceptible to suffer in competition. Water colour clearly affected visually-oriented perch feeding and growth negatively, but did not affect roach. High water colour could thus favour roach over perch in humic lakes in competition for the same food resources. The prolonged benthic feeding phase of perch resulting from the increased water colour could increase intraspecific competition in perch populations and may result in a partial bottleneck in growth for perch. Moreover, water colour may act as a proximate factor behind the population dependency of sexual growth dimorphism in perch.

7. Future studies

Global climatic warming is expected to be greatest in the boreal and subarctic regions (Houghton et al. 1996). These areas contain one third of the world's soil carbon pool and supply most of the dissolved organic carbon (DOC) entering boreal lakes (Mulholland & Kuenzler 1979; Gorhan 1991). The present study suggests that high levels of water colour may have cascading effects on fish populations: e.g. inter- and intraspecific competition and sexual growth dimorphism in fish through variations in feeding efficiency. Therefore, it is crucial to study in further detail the relationship between environmental change, female fish growth, fry production and survival at the population, community and ecosystem levels, particularly the role played by increasing environmental change.

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